

Characterization of restricted area searching behavior following consumption of prey and non-prey food in a cursorial spider, *Hibana futilis*

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Abstract

Cursorial spiders are important predators of crop pests in a variety of agricultural systems. Their survivorship, growth, and fecundity can be enhanced by the consumption of extra-floral nectar. We recently showed that *Hibana futilis* (Banks) (Araneae: Anyphaenidae) engages in restricted area search following contact with nectar, is stimulated by nectar aroma, and can learn to recognize novel aroma cues. Studies have shown that *H. futilis* is also responsive to solvent extracts of the eggs and scales of the corn earworm, *Helicoverpa zea* Boddie (Lepidoptera: Noctuidae), one of its primary prey insects in cotton. The arrestment behavior of cursorial spiders following consumption of prey and non-prey food has not been characterized. In the present study, the responses of spiders were measured following consumption of prey (*H. zea* eggs) or non-prey (droplets of dilute honey) food items and compared with individuals tested without food items. The food items were presented to the spiders in test arenas constructed from the top of an inverted glass Petri dish cover. A combination of real time and recorded observations were made via a video camera attached to a computer. The behaviors and movement patterns of individual spiders were analyzed with behavioral tracking software. Significant differences in the behaviors and motion paths of spiders tested in the different treatments were observed. *Hibana futilis* displayed significantly more dispersal behavior on a blank test arena, than on test arenas supplied with honey droplets or moth eggs. Likewise, spiders tested on the blank arena crawled faster and their motion paths were significantly less tortuous than those of spiders tested in the arenas with honey or moth eggs. Following consumption of both the honey droplets and moth eggs, spiders showed elevated levels of restricted area search and lowered levels of dispersal behavior. The analysis showed that these spiders could crawl rapidly for extended distances. Behaviors such as restricted area search and learned recognition of food-based stimuli would facilitate efficient location of the food resources needed to maintain their high activity levels.

Introduction

The consumption of plant-based food, such as nectar and pollen, has been shown to enhance the activity levels, survivorship, development, and fecundity of omnivorous predatory arthropods (Jervis & Kidd, 1996; Landis et al., 2000; Wäckers et al., 2005). The diet of certain non-web building spiders that wander in search of prey also extends to floral and extrafloral nectar

(Pollard et al., 1995; Ruhren & Handel, 1999; Jackson et al., 2001; Taylor, 2004; Taylor & Pfannenstiel, 2008). The chemosensory stimuli associated with the various types of plant and animal nutritional resources utilized by omnivorous arthropods can vary spatially, temporally, and with respect to their chemical and physical characteristics (Bell & Cardé, 1984). To successfully exploit the range of animal and plant-based resources available to them, omnivores must be capable of responding efficiently to a wide range of disparate stimuli that indicate the presence of these resources (Hagen et al., 1976; Lewis & Takasu, 1990; Harris & Fos-

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ter, 1995; de Boer & Dicke, 2005; Olson et al., 2005; Zhan et al., 2008).

The utilization of various types of kairomones by spiders that stalk or ambush their prey (e.g., wolf- and jumping spiders) is well-known (Persons & Uetz, 1996; Clark et al., 2000; Persons & Rypstra, 2000; Jackson et al., 2002, 2005), and studies of their perception of prey-associated stimuli have revealed that their cognitive abilities are very sophisticated (Persons & Uetz, 1997; Krell & Krämer, 1998; Jackson et al., 2002, 2005; Jackson & Li, 2004; Vandersal & Hebets, 2007). The ability of spiders to recognize chemosensory stimuli associated with plant-based food or plants themselves has started to receive attention. Heiling et al. (2004) showed that crab spiders respond differentially to odor and visual cues emitted by flowers, where they lie in ambush for prey insects. In this case the crab spiders were adept at responding to plant signals that indicated the presence of foraging sites rather than food directly. Likewise, Vasconcellos-Neto et al. (2007) showed that certain lynx spiders are closely associated with plants with glandular trichomes, to which small prey insects adhere and become trapped. Ruhren & Handel (1999) showed that jumping spiders remain longer on plants with extrafloral nectaries than nectariless plants.

There are a number of cursorial spider species (Araneae), such as *Hibana futilis* (Banks) (Anyphaenidae), *Hibana arunda* Platnick, and *Cheiracanthium inclusum* Hentz (Miturgidae), which commonly occur in a variety of crops in the southern USA (Breene et al., 1993; Amalin et al., 2001; Michaud, 2004; Renouard et al., 2004; Pfannenstiel, 2005). These spiders actively crawl on the foliage of herbaceous and woody plants and are important predators of small soft-bodied insects and the eggs of agricultural pests such as the corn earworm, *Helicoverpa zea* Boddie (Lepidoptera: Noctuidae) (Breene et al., 1993; Amalin et al., 2001; Michaud, 2004; Renouard et al., 2004; Pfannenstiel, 2005, 2008). Immature *C. inclusum* perceive contact kairomones from *H. zea* eggs and scales (Ruiz, 2006). These spiders also feed extensively on extrafloral nectar. Surveys conducted in south Texas cotton fields demonstrated that at least 30% of *H. futilis* individuals tested with the cold anthrone test had recently fed on cotton extrafloral nectar (Taylor & Pfannenstiel, 2008). Recently, we showed that immature *H. futilis* enter into restricted area search (i.e., become arrested) following contact with dilute honey (Patt & Pfannenstiel, 2008). Restricted area searching behaviors are exhibited by a searching animal when it detects a resource cue, and comprises a slowing down or stopping of locomotion (orthokinesis) and/or a change

in the rate of turning (klinokinesis) (Dethier, 1976; Bell, 1991). Tested in behavioral arenas that contained both contact stimuli (aqueous sucrose droplets) and olfactory stimuli (honey aroma), *H. futilis* located simulated extrafloral nectaries more quickly than when tested in arenas that lacked one or the other of this pair of stimuli, further indicating that *H. futilis* is stimulated by nectar aroma and can learn to recognize novel nectar aromas (Patt & Pfannenstiel, 2008). We attributed the decrease in location time of the simulated extrafloral nectaries to a combination of olfactory stimulation and restricted area search. Clearly, extrafloral nectar is an important food resource for *H. futilis* and this spider possesses sensory and behavioral traits that facilitate its recognition and location.

In the current study, we tested the capability of a video-based behavioral assay to characterize and compare the restricted area search responses of *H. futilis* following consumption of prey (moth eggs) and non-prey (diluted honey) food. Quantifying the behavioral components of restricted area search and the motion paths of *H. futilis* is part of a broader study aimed at evaluating the relative behavioral responses of cursorial spiders to prey and non-prey foods.

Materials and methods

Spiders

All tests used third and fourth instars of *H. futilis* that were collected from pigweed, *Amaranthus palmeri* (S. Watson) (Amaranthaceae), and cotton, *Gossypium hirsutum* L. (Malvaceae) at the USDA-ARS experimental farm in Weslaco, TX, USA. Third instar *H. futilis* readily consume moth eggs and artificial nectar and respond ideally on the circular test arenas (Patt & Pfannenstiel, 2008). When collected, all individuals were well fed as indicated by the round, large shape of their abdomens. Spiders were transferred to individual Petri dishes and kept in an incubator under a L14:D10 regime at $26 \pm 1^\circ\text{C}$. Water was provided continuously with a moistened cotton wick. Because *H. futilis* is nocturnal (Pfannenstiel, 2008), they were maintained on a reverse photcycle to permit daytime testing (during scotophase 10:00 to 17:00 hours). Spiders were provided with corn earworm eggs ad libitum.

Behavioral observations

A test arena constructed from the top lid of a glass Petri dish (10 cm diameter) was used to measure the localized searching behavior of immature *H. futilis* following consumption of either prey- or non-prey food. Corn earworm eggs were used as the prey food item and drop-

lets of artificial nectar [12.5% aqueous honey solution (vol/vol)] were used as the non-prey food item. As a control, observations were also made of spiders placed on a blank Petri dish without food items. When placed on a Petri dish lid, *H. futilis* tend to move to the dish perimeter and then crawl along the edge (Patt & Pfannenstiel, 2008). However, when engaged in restricted area search, their thigmotactic behavior diminishes. In the observations described below, either moth eggs or nectar droplets were positioned along the dish edge so that the spiders could quickly locate them and subsequently search the remainder of the dish (Patt & Pfannenstiel, 2008).

For each observation, a spider was presented with either three tiny nectar droplets (2 μ l each) or three corn earworm eggs. Each nectar droplet was approximately the same size as a moth egg. The food items were placed equidistant from one another along the dish edge. The eggs were anchored to the dish with small droplets of white glue to prevent the spiders from carrying the eggs and confounding analysis of their movement patterns. The spiders remained stationary while feeding on the nectar droplets.

The observations were recorded with a video camera (Panasonic CCTV camera, model WV-CP450; Matsushita Electric Industrial, Yokohama, Japan) fitted with a macro zoom lens (12.5–75 mm, F1.5; Navitar, Rochester, NY, USA) and a 10 mm extension tube (Pentax; Hoya, Tokyo, Japan). The camera was connected to a desktop computer (Optiplex 745; Dell, Round Rock, TX, USA) equipped with EthoVision behavioral recording and tracking software (v3.0, Noldus Information Technology, Wageningen, The Netherlands). The camera was attached to a flexible mounting arm (PanaVise Products, Reno, NV, USA) so that the lens was positioned ca. 25 cm above the Petri dish.

For each observation, an individual spider was released onto the dish center and its subsequent movements were recorded. Only spiders that were actively moving within their culture dishes when inspected at testing time were used in the experiments. Individuals that were hidden in their silken retreat tubes or otherwise quiescent were not selected. To improve their responsiveness during the experiments, spiders were starved for 24–120 h prior to testing (JM Patt, unpubl.). Some individuals were not responsive on the assay dish until they had been food-deprived for several days. As wild-caught spiders were used in the tests, they likely varied with respect to gut load and nutritional state when collected. A posteriori test indicated that starvation times of up to 4 or 5 days did not negatively affect these spiders' performance during the tests (see Results).

At least 30 individuals were tested on each treatment and an effort was made to test each individual spider on all three treatments over the course of the study. However, not all of the spiders survived long enough to be tested on all three treatments. Twenty individuals were observed on all three treatments, whereas 12 individuals were observed on the blank and either the honey droplet or moth egg treatments, and 11 individuals were observed on only one treatment.

Because the spiders became very agitated when handled, each individual was anaesthetized by gentle chilling for 60–180 s just prior to testing (Patt & Pfannenstiel, 2008). Chilling was accomplished by transferring a culture dish with its spider from the incubator into a -4°C freezer. Once anaesthetized, the spider was immediately transferred from its culture dish to the arena with an artist's paintbrush. Spiders that did not become active within 90 s after transfer to the arena were returned to the incubator.

The Petri dish used for the observations was placed inside a larger Petri dish (15 cm diameter \times 1.5 cm high) filled approximately 5 mm deep with water to form a moat and discourage spiders from leaving the observation area. Observations began when a spider began to move following its release. They were concluded when the spider either left the arena or reached a predetermined time limit. Timing was suspended whenever the spiders fed so that feeding time was not included in the overall time limit. For spiders tested on arenas with either moth eggs or honey droplets, a time limit of 360 s was selected. Pre-trial tests indicated that this time period was optimal with respect to measuring the spiders' foraging behavior. To control for overall time spent on the arena, the time limit for the blank treatment was increased to 480 s to compensate for time that would have otherwise been spent feeding in the other treatments. Observations were excluded from the analysis if the spiders left the arena within 60 s or did not consume the food items after encountering them.

Hibana futilis initiates ballooning when exposed to an air current (JM Patt, unpubl.). To reduce the amount of air circulation around the arena, the observer wore a paper mask and the tests were conducted inside an inactive fume hood fitted with a black theatre curtain cloth to cover the opening. The observations were conducted in semi-darkness (ambient light <5 lux) at room temperature ($28 \pm 1^{\circ}\text{C}$). Illumination for video recording was provided by the screen of a laptop computer that was open fully so that the screen faced upward. The Petri dish was placed directly on top of the screen. The laptop computer was programmed to display a PowerPoint (Microsoft, Redmond, WA, USA) slide with a dim

(75 lux) white background. Backlighting improved the accuracy of the recordings by eliminating shadows and light reflections from the surface of the Petri dish and providing sharp, high contrast images of the spiders that permitted the software to distinguish the spider from the background. The surface of the monitor screen was the same as the ambient room temperature (30 °C). The monitor of the desktop computer emitted some additional background light. The spiders behaved normally when placed under these semi-dark conditions.

A combination of camera and dish placement arrangement and lens aperture and zoom settings were used to provide a focused image that included both the spider and the entire surface of the Petri dish. The image detection settings in the software were adjusted to optimize the contrast between the spider and background. Image discrimination was achieved in the software's grayscale mode with the minimum size detection threshold set at 40 pixels. Because the spiders could move rapidly across the dish, the EthoVision sample rate was set at 30 samples s^{-1} . An image erosion and dilation filter was used to decrease the effect of the spiders' 'leginess' on the software's ability to accurately track their centers.

Behavioral parameters that are commonly used to measure path movement pattern (Bell, 1991) were used to characterize the spiders' restricted area search responses. For each observation, the parameters calculated by the software included: total distance moved (cm), turn angle (degrees), and velocity ($cm\ s^{-1}$). Because the spiders display thigmotaxis along the dish edge, the relative percentage of time spent along the edge vs. the interior of the dish was calculated as a possible means of providing information about the relative intensity of restricted area search observed in the different treatments. The software was programmed to differentiate the Petri dish into a perimeter zone that extended 10 mm from the dish edge and a center zone that comprised the remainder of the dish (76 mm diameter). This enabled us to calculate the amount of time the spiders spent in each zone.

To further characterize the spiders' response to prey vs. non-prey food, a number of other key behaviors were measured during each observation. In addition to restricted area search, these included crawling, dispersal behavior, and sitting. Crawling was indicated by the absence of counter-turning and movement reversals while a spider was crawling, i.e., its movement was primarily in a forward direction, it displayed little or no deviation from a straight-line trajectory, and did not hold its fore tarsi in any particular posture. Local search was indicated by counter-turning and movement reversals that occurred more or less continuously while

crawling. Dispersal behavior was indicated by ballooning postures (Turnbull, 1973) in which the abdomen and/or fore tarsi were upraised.

The manual event recorder module of EthoVision was used to record the spiders' behavior during the observations. Compilation of behavioral data gathered by the software enabled us to calculate the percentage of time the spiders spent engaged in each behavior. The total amount of time that each spider fed was subtracted from the total observation time. This corrected total observation time was used to calculate the percentage of time the spiders' spent engaged in non-feeding behaviors. Because the spiders' images displayed on the computer monitor were too small to discern particular behaviors, surgical magnifying glasses (Designs for Vision, Ronkonkoma, NY, USA), with $3\times$ magnification and a working distance of ca. 45 cm, were used to observe the spiders without disturbing them.

Statistical analysis

Motion path and behavioral data were analyzed with the Kruskal-Wallis test (Zar, 1999) and when significant differences ($\alpha = 0.05$) were indicated, a multiple comparison test using ranked sums and an experiment wide error rate described by Daniel (1990) was used to make pairwise comparisons (Excel; Microsoft, Redmont, WA, USA).

Results

Following consumption of moth eggs or honey droplets *H. futilis* spent a proportionately significant amount of time engaged in restricted area search, whereas spiders tested on the blank arena did not display restricted area search. There was no difference in the percentage of time spent in restricted area search in spiders tested on the arenas with honey droplets or moth eggs (Dunn's rank sum test: moth eggs vs. honey droplets: $z < 0.001$, ns) (Figures 1 and 2). Accordingly, the degree of turning was significantly greater in honey- and egg-fed spiders than in unfed spiders in the blank treatment (Kruskal-Wallis test, turn angle: $H = 12.179$, d.f. = 2, $P < 0.001$; Dunn's rank sum test: blank vs. moth eggs: $z = 54$, $P < 0.001$; blank vs. honey droplets: $z = 21$, $P = 0.01$) (Figure 3A). Likewise, the duration of crawling and dispersal behavior was significantly longer in the blank treatment than in either the moth egg or honey droplet treatments (Kruskal-Wallis test, crawling: $H = 70.523$, d.f. = 2, $P < 0.001$; dispersal behavior: $H = 7.546$, d.f. = 2, $P = 0.026$) (Figure 2).

The spiders typically moved very quickly over relatively large distances on the test arenas (Figure 3B). This

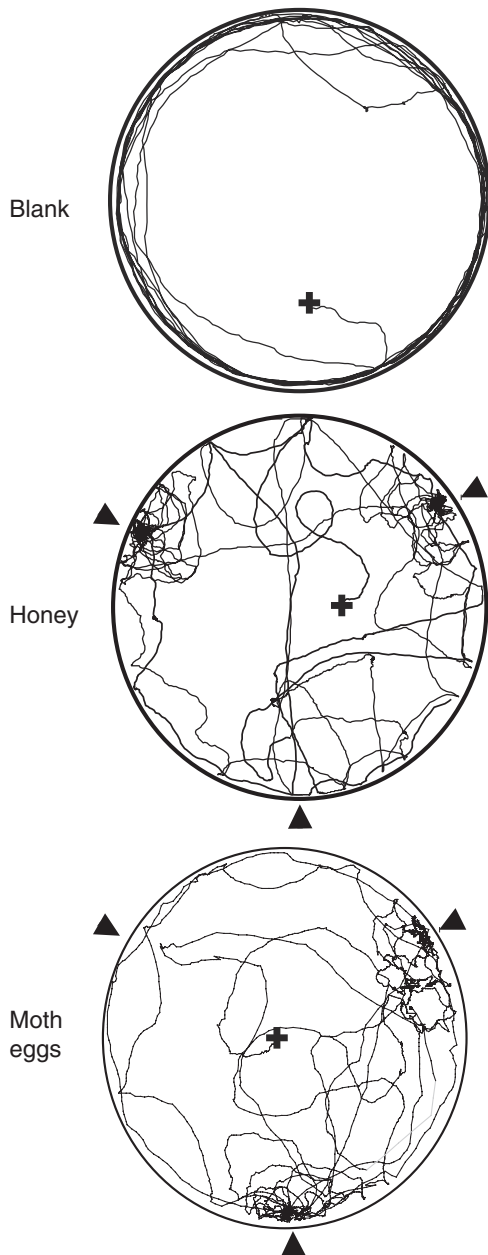


Figure 1 Representative motion tracks of *Hibana futilis* on test arenas with different treatments. Arrows indicate approximate location of food items along the dish perimeter. Path origin is indicated by +.

observation correlates with field observations in which the spiders are typically seen running quickly across foliage (RS Pfannenstiel, unpubl.). The distances covered by spiders from the different treatments were similar (Kruskal-Wallis test: $H = 0.104$, d.f. = 2, $P = 0.96$) (Figure 3B) although the velocity of the spiders tested in the blank treatment was significantly greater than

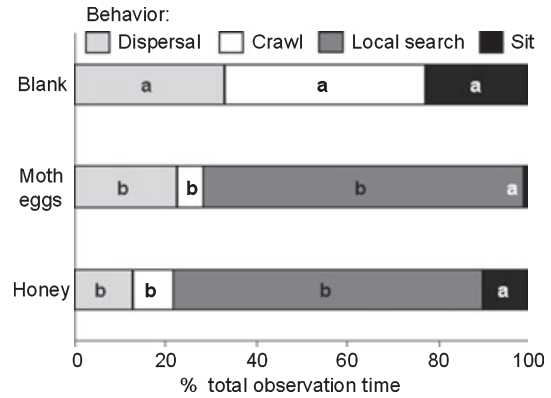


Figure 2 Time allocation (percent) of individual *Hibana futilis* behaviors. Means marked by different letters within behavior categories are significantly different at the following levels: dispersal behavior, $P < 0.026$ between blank and treatments with honey droplets or moth eggs; local search, $P < 0.001$; and crawling, $P < 0.001$ (Kruskal-Wallis test; $n = 30$ spiders per treatment).

those in the other treatments (Kruskal-Wallis test: $H = 37.901$, d.f. = 2, $P < 0.001$; Dunn's rank sum test: blank vs. moth eggs: $z = 49$, $P < 0.001$; blank vs. honey droplets: $z = 17$, $P = 0.05$) (Figure 3C). This is likely due to the lack of turning observed in spiders on the blank arena. The velocity of the spiders in the honey treatment was greater than that of those in the moth egg treatment (Dunn's rank sum test: honey vs. eggs: $z = 32$, $P = 0.001$), which is also probably related to the lower degree of turning observed in the honey treatment relative to that of the moth egg treatment (Dunn's rank sum test: honey droplets vs. moth eggs: $z = 32$, $P < 0.001$).

Spiders from the various treatments spent similar amounts of time in the center of the test dish (Kruskal-Wallis test, $H = 1.524$, d.f. = 2, $P = 0.55$). Although the spiders in the blank treatment displayed strong thigmotaxis along the edge of the test arena, they also frequently moved from one edge of the dish to the other, crisscrossing the center of the arena as they did so (Figure 1). Much of the restricted area search occurred in the perimeter zone of the test arena.

Post-priori tests showed that the behavior of the spiders did not change as a function of pre-test starvation time (Kruskal-Wallis test; turn angle: blank control: $H = 3.326$, d.f. = 2, $P = 0.30$; honey: $H = 1.567$, d.f. = 4, $P = 0.61$; moth eggs: $H = 3.664$, d.f. = 4, $P = 0.55$. Distance moved: blank control: $H = 3.450$, d.f. = 2, $P = 0.31$; honey: $H = 0.066$, d.f. = 3, $P = 0.91$; moth eggs: $H = 3.853$, d.f. = 4, $P = 0.57$. Velocity: blank control: $H = 3.174$, d.f. = 2, $P = 0.29$; honey:

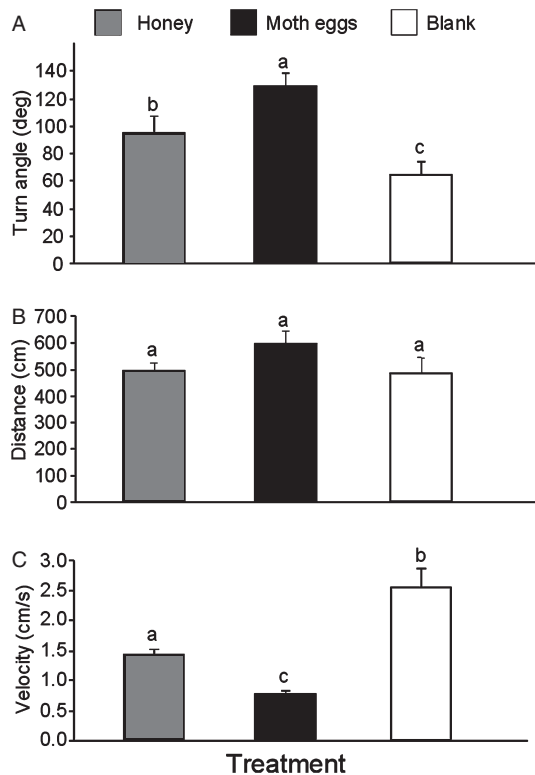


Figure 3 Mean (+ SEM) behavioral and track parameters. (A) Turn angle. Means marked by different letters are significantly different at the following levels: honey droplets vs. moth eggs, $P < 0.001$; honey droplets vs. blank, $P < 0.05$; moth eggs vs. honey droplets, $P = 0.01$ (Kruskal–Wallis test & Dunn’s rank sum test). (B) Distance traveled. (C) Velocity. Means marked by different letters are significantly different at the following levels: honey droplets vs. moth eggs, $P < 0.001$; blank vs. honey droplets, $P = 0.05$; blank vs. moth eggs, $P < 0.001$ (Kruskal–Wallis test). In all treatments: $n = 30$.

$H = 0.057$, d.f. = 3, $P = 0.78$; moth eggs: $H = 7.715$, d.f. = 4, $P = 0.09$).

Discussion

The combination of live observations followed by analysis of video recordings with EthoVision permitted characterization and comparison of restricted area search in cursorial spiders after they fed on prey and non-prey food items. Both motion paths and behavioral transitions were effectively recorded and examined with this method. Backlighting the transparent test arenas with the screen of a laptop computer provided sufficient contrast between the spiders and the transparent surface of the test arenas to permit the software to track the fast-moving spiders. Backlighting also obviated any potential

problems with the software that would have been caused by reflections from the arena surface due to illumination from above. The spiders appeared to behave in a normal fashion under the illumination conditions provided by the laptop computer screen.

Significant differences in behavior and motion paths were observed in spiders exposed to food vs. those that tested on the blank arena. Compared with spiders released on test arenas with honey droplets or moth eggs, *H. futilis* tested on the blank arena crawled faster (i.e., higher orthokinesis), engaged in significantly more dispersal behavior and non-differentiated crawling, and turned less frequently (i.e., decreased klinokinesis). Consumption of a single moth egg or honey droplet was followed by prolonged restricted area search that was indicated by decreased velocity (i.e., lower orthokinesis), increased levels of turning (i.e., increased klinokinesis), and decreased dispersal behavior.

These results demonstrated that *H. futilis* engaged in restricted area search following consumption of a small amount of either prey or non-prey food and provides further evidence for the importance of non-prey foods in its diet. It is not clear whether *H. futilis* responded more strongly to prey or non-prey food. Spiders that fed on moth eggs turned more frequently and moved more slowly than spiders that fed on honey. However, since the nutritional content of the two treatments was not controlled, we cannot say that it was the consumption of prey per se that resulted in a higher level of restricted area search than consumption of a non-prey food. To determine this question, further experiments are needed in which selection of food items with known nutritional values is measured. Such experiments would help determine whether qualitative differences in food values result in differentiated behavioral responses towards prey- and non-prey foods, and if selection of different types of foods is dictated by an internal ‘nutritional target’ mechanism that helps ensure that these spiders maintain an optimum balance of nutrients (Raubenheimer & Simpson, 1993; Simpson & Raubenheimer, 1996; Behmer et al., 2001; Simpson et al., 2002, 2003; Mayntz et al., 2005).

As well, further studies are needed to determine whether consumption of food is necessary to elicit restricted area search or if *H. futilis* will respond to semiochemicals without feeding. In a previous study, we found that *H. futilis* responded to nectar odor only after it had consumed a small amount of sucrose (Patt & Pfannenstiel, 2008). However, Ruiz (2006) showed that *Cheiracanthium inclusum* Hentz, another cursorial spider sympatric with *H. futilis*, was stimulated by solvent extracts of the eggs and scales of *H. zea*. Response to kairomones associated with sessile prey, such as moth

eggs, may be an important component of the foraging behavior of cursorial spiders (Ruiz, 2006).

Regardless of treatment, *H. futilis* exhibited a capacity for moving quickly over relatively large distances. Mean distances of ca. 500–600 cm accompanied by mean crawling velocities up to 2.5 cm s^{-1} were recorded during observation periods that typically lasted from 240 to 260 s. These values seem to correspond to numerous field observations in which the spiders' typical foraging behavior consisted of prolonged bouts of rapid crawling over extensive portions of foliage (RS Pfannenstiel, unpubl.). The mode of foraging used by *H. futilis* probably has a high energetic cost and frequent consumption of sugars from nectar or honeydew may enhance the spiders' ability to maintain the energetics required for this type of foraging. Behavioral adaptations such as restricted area search and learned recognition of food-based stimuli (Patt & Pfannenstiel, 2008) are likely to increase cursorial spiders' ability to efficiently search for and locate food in the complex environment of plant foliage. Augmentation of non-prey foods (i.e., sugar sprays and yeast-based food supplements) may be effective means to enhance the survivorship and development of cursorial spiders and other predaceous omnivores in agroecosystems (Wäckers et al., 2005; Wade et al., 2008).

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References

- Amalin DM, Reiskind J, Pena JE & McSorley R (2001) Predatory behavior of three species of sac spiders attacking citrus leafminer. *Journal of Arachnology* 29: 72–81.
- Behmer ST, Raubenheimer D & Simpson J (2001) Frequency-dependent food selection in locusts: a geometric analysis of the role of nutrient balancing. *Animal Behaviour* 61: 995–1005.
- Bell WJ (1991) *Searching Behavior: The Behavioral Ecology of Finding Resources*. Chapman & Hall, London, UK.
- Bell WJ & Cardé RT (1984) *Chemical Ecology of Insects*. Sinauer Associates, Sunderland, MA, USA.
- de Boer JG & Dicke M (2005) Information use by the predatory mite *Phytoseiulus persimilis* (Acari: Phytoseiidae), a specialized natural enemy of herbivorous spider mites. *Applied Entomology and Zoology* 40: 1–12.
- Breene RG, Dean DA, Nyffeler M & Edwards GB (1993) *Biology, Predation Ecology, and Significance of Spiders in Texas Cotton Ecosystems with a Key to Species*. The Texas Agricultural Experiment Station, College Station, TX, USA.
- Clark RJ, Jackson RR & Cutler B (2000) Chemical cues from ants influence predatory behavior in *Habrocestum pulex*, an ant-eating jumping spider (Araneae, Salticidae). *Journal of Arachnology* 28: 309–318.
- Daniel WW (1990) *Applied Nonparametric Statistics*, 2nd ed. PWS-KENT Publishing, Boston, MA, USA.
- Dethier VG (1976) *The Hungry Fly*. Harvard University Press, Cambridge, MA, USA.
- Hagen KS, Greany P, Sawall EF & Tassan RL (1976) Tryptophan in artificial honeydews as a source of an attractant for adult *Chrysoperla carnea*. *Environmental Entomology* 5: 458–468.
- Harris MO & Foster SP (1995) Behavior and integration. *Chemical Ecology of Insects*, Vol. 2 (ed. by RT Cardé & WJ Bell), pp. 3–46. Chapman & Hall, New York, NY, USA.
- Heiling AM, Cheng K & Herberstein ME (2004) Exploitation of floral signals by crab spiders (*Thomisus spectabilis*, Thomisidae). *Behavioral Ecology* 15: 321–326.
- Jackson RR & Li D (2004) One-encounter search-image formation by araneophagic spiders. *Animal Cognition* 7: 247–254.
- Jackson RR, Pollard SD, Nelson XJ, Edward GB & Barrion AT (2001) Jumping spiders (Araneae: Salticidae) that feed on nectar. *Journal of Zoology* 255: 25–29.
- Jackson RR, Clark RJ & Harland DP (2002) Behavioral and cognitive influences of kairomones on an araneophagic jumping spider. *Behavior* 139: 749–775.
- Jackson RR, Nelson XJ & Sune GO (2005) A spider that feeds indirectly on vertebrate blood by choosing female mosquitoes as prey. *Proceedings of the National Academy of Sciences of the USA* 102: 15155–15160.
- Jervis M & Kidd N (1996) *Insect Natural Enemies. Practical approaches to their study and evaluation*. Chapman & Hall, London, UK.
- Krell FT & Krämer F (1998) Chemical attraction of crab spiders (Araneae, Thomisidae) to a flower fragrance component. *Journal of Arachnology* 26: 117–119.
- Landis DA, Wratten SD & Gurr GM (2000) Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology* 45: 175–201.
- Lewis WJ & Takasu K (1990) Use of learned odours by a parasitic wasp in accordance with host and food needs. *Nature* 348: 635–636.
- Mayntz D, Raubenheimer D, Saloman M, Toft S & Simpson S (2005) Nutrient-specific foraging in invertebrate predators. *Science* 307: 111–113.

- Michaud JP (2004) Natural mortality of Asian citrus psyllid (Homoptera: Psyllidae) in central Florida. *Biological Control* 29: 260–269.
- Olson DM, Takasu K & Lewis WJ (2005) Food needs of adult parasitoids: behavioral adaptations and consequences. *Plant-provided Food for Carnivorous Insects: A Protective Mutualism and its Applications* (ed. by FL Wäckers, PCJ van Rijn & J Bruin), pp. 137–147. Cambridge University Press, Cambridge, UK.
- Patt JM & Pfannenstiel RS (2008) Odour-based recognition of nectar in spiders. *Entomologia Experimentalis et Applicata* 127: 64–71.
- Persons MH & Rypstra AL (2000) Preference for chemical cues associated with recent prey in the wolf spider *Hogna helluo* (Araneae: Lycosidae). *Ethology* 106: 27–35.
- Persons MW & Uetz GW (1996) The influence of sensory information on patch residence time in wolf spiders (Araneae: Lycosidae). *Animal Behaviour* 51: 1285–1293.
- Persons MH & Uetz GW (1997) Foraging patch residence time decisions in wolf spiders: Is perceiving prey as important as eating prey? *Ecoscience* 4: 1–5.
- Pfannenstiel RS (2005) Nocturnal predators and their impact on lepidopteran eggs: what we don't see does help us! *Proceedings of the 2nd International Symposium on Biological Control of Arthropods* (ed. by MS Hoddle), pp. 463–471. US Forest Service, FHTET-2005-08, Morgantown, WV, USA.
- Pfannenstiel RS (2008) Spider predators of lepidopteran eggs in south Texas field crops. *Biological Control* 46: 202–208.
- Pollard SD, Beck MW & Dodson GN (1995) Why do male crab spiders drink nectar? *Animal Behaviour* 49: 1443–1448.
- Raubenheimer D & Simpson S (1993) The geometry of compensatory feeding in the locust. *Animal Behaviour* 45: 953–964.
- Renouard JJ, Creamer R & Richman DB (2004) Gut content analysis of the spider *Hibana incursa* (Araneae: Anyphaenidae) using serological methods. *Southwestern Entomologist* 29: 91–97.
- Ruhren S & Handel SN (1999) Jumping spiders (Salticidae) enhance the seed production of a plant with extrafloral nectaries. *Oecologia* 116: 227–230.
- Ruiz RI (2006) Response of *Cheiracanthium inclusum* Spiderlings to Kaironomes Associated with the Eggs and Scales of their Prey, the Cotton Bollworm. MSc Thesis, University of Texas at Pan American, Edinburg, TX, USA.
- Simpson S & Raubenheimer D (1996) Feeding behavior, sensory physiology and nutrient feedback: a unifying model. *Entomologia Experimentalis et Applicata* 80: 55–64.
- Simpson SJ, Raubenheimer D, Behmer S, Whitworth A & Wright GA (2002) A comparison of nutritional regulation in solitary- and gregarious-phase nymphs of the desert locust *Schistocerca gregaria*. *Journal of Experimental Biology* 205: 121–129.
- Simpson S, Sibly R, Lee KP, Behmer S & Raubenheimer D (2003) Optimal foraging when regulating intake of multiple nutrients. *Animal Behaviour* 68: 1299–1311.
- Taylor RM (2004) Plant Nectar Contributes to the Survival, Activity, Growth, and Fecundity of the Nectar-feeding Wandering Spider *Cheiracanthium inclusum* (Hentz) (Araneae: Miturgidae). PhD Dissertation, Ohio State University, Columbus, OH, USA.
- Taylor RM & Pfannenstiel RS (2008) Nectar feeding by wandering spiders on cotton plants. *Environmental Entomology* 37: 996–1002.
- Turnbull AL (1973) Ecology of the true spiders (Araneomorphae). *Annual Review of Entomology* 11: 175–183.
- Vandersal ND & Hebets EA (2007) Cross-modal effects on learning: a seismic stimulus improves color discrimination learning in a jumping spider. *Journal of Experimental Biology* 210: 3689–3695.
- Vasconcellos-Neto J, Romero GQ, Santos AJ & Dippenaar-Schoeman AS (2007) Associations of spiders of the genus *Peucetia* (Oxyopidae) with plants bearing glandular hairs. *Biotropica* 39: 221–226.
- Wäckers FL, van Rijn PCJ & Bruin J (eds) (2005) *Plant-provided Food for Carnivorous Insects: A Protective Mutualism and its Application*. Cambridge University Press, Cambridge, UK.
- Wade M, Zalucki MP, Wratten SD & Robinson KA (2008) Conservation biological control of arthropods using artificial food sprays: Current status and future challenges. *Biological Control* 45: 185–199.
- Zar JH (1999) *Biostatistical Analysis*. Prentice-Hall, Upper Saddle River, NJ, USA.
- Zhan RK, James DG, Midega CAO & Pickett JA (2008) Chemical ecology and conservation biological control. *Biological Control* 45: 210–224.